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ON THE HOMOLOGIES AND EARLY HISTORY OF THE
LIMBS OF VERTEBRATES.

BY JOHN A. RYDER.

I. The imperfect serial homology of the limbs of Vertebrates.

That any one should seriously question the complete homology of the anterior and posterior pairs of limbs as found developed in the great classes;—Mammals, Birds, Reptiles, Amphibia and Lyrifera, (*Ichthyes*, or all fish-like vertebrates, except the Lampreys and Hags,) is, perhaps, at first thought, a somewhat startling proposition. The fact that there is an imperfect homology or a want of exact morphological equivalency between the parts of the same pairs of limbs in different forms, has been tacitly admitted by such of the transcendental anatomists as Gervais and Gegenbaur, and those anatomical philosophers who have been influenced by their *a priori* methods, in developing which, certain suppositions had to be made, which at the time, could not be or were not verifiable or refutable from data supplied by general ontogeny or embryology. The case stands differently to day. Since Gervais and Gegenbaur wrote on the theory of the limbs, owing mainly to the remarkably fruitful labors of Haeckel, Balfour and Dohrn, the great morphological problems presented for solution by the organizations of the diverse classes of vertebrata, have presented themselves under entirely new aspects. These are not only momentous as affording a key to the interpretation of the anatomy of the adults of the different types, but also as throwing a not inconsiderable amount of light upon the relations and taxonomy of the major groups.

That the paired limbs have been derived from some common, simple ancestral form of limb, is, I cannot help but believe, proved by the following general truths:—

1. In the most undeveloped condition, the first traces of the paired limbs of all vertebrates, find formal expression as low longitudinal, lateral projections of the body, and lie in a plane parallel with that of the axis of the latter. This fact originally observed by K. E. von Baer, has in part afforded J. K. Thacher, F. M. Balfour, and St. G. Mivart, the basis for a theory of the development of the paired limb, but it remained for A. Dohrn to discover that there existed a continuous series of vestigiary structures in certain forms which connected the anterior and posterior limbs together into a

continuous chain of serially homologous or homodynamous elements. These lateral elements of the limb, are therefore, to be regarded as metameric structures, in that they correspond with the metamerism of the body. The fore and hind limbs are, therefore, and presumably in all forms, to be regarded as directly or indirectly differentiated from a *single* pair of lateral folds, it matters not in what way the process may be obscured by extreme secondary modifications or specializations of development.

2. The subsidiary doctrines which confirm the preceding, may be stated as follows:—

a. The lowest truly limb-bearing vertebrates are the only ones in which the lateral folds, from which both pairs of limbs are derived, are continuous or which show a continuous series of limb-buds under the integument along either side of the embryo.

b. This lowest limb-bearing group is also the only one in which the branches of the paired spinal nerves, which pass out to the metamERICALLY repeated limb-buds, ever form a continuous series, or in which the paired limbs maintain their primordial horizontal position.

c. The group here referred to, the *Elasmobranchii*, is, moreover, primitive in many other ways, especially as respects:—(1) or histological development, in that no parosteal or membrane bones are developed, as in the higher types, and, (2) or morphological development, in that the branchiæ are at first naked, with no operculæ in the adult; skeleton principally cartilaginous; distal part of vertical fins and paired limbs, supported and stiffened by actinotrichia above, with shagreen or dermal spines covering them; teeth generally successional from a thecal fold, and transitional to the spines or denticles found in the common external tegumentary covering of the body; no air bladder or pneumatic apparatus; shoulder and pelvic girdles simple; jaws and mandibular arch simple, suspended directly to the skull; a wide, spiracular, branchiferous cleft; generative and renal apparatus of a primitive type; muscular buds, which are thrust into the median and paired limb-folds, with traces of a lumen or cavity, which has been derived from the cavity found in the myotomes, from which the muscular buds have been derived as outgrowths or diverticula.

This evidence is quite sufficient for us at present to build upon, for the Ascidians, Leptocardians and Enteropneusta have no claim, as based either upon their morphology or upon their ontogeny, to

be regarded as forms ancestrally or phyletically related in a direct line to the limb-bearing vertebrates. It will probably be best to regard all of these, including the Lampreys and Hags, as extreme retrograde modifications or as adumbrations of something higher in the Chordate series, and indeterminate in every respect to their exact position with reference to the great limb-bearing phylum. The *Elasmobranchii*, therefore, alone remain as a point of departure.

It is not possible to develop a rational interpretation of the inexact homology of the paired limbs of the various types, in which it may be suspected to exist, unless we start with the *Elasmobranchs*, because, in the latter only, do we find the limbs in a condition which there is every reason to regard as the most primitive. The principal mark of this primitiveness is, as before stated, the continuity, at a certain stage, of the limb-rudiments, the elements of which are, moreover, metamerically repeated, that is, they recur as out-growths from each and every successive myotome of the series underlying the paired integumentary folds, from portions of which, together with a greater or lesser number of the underlying muscular limb-buds and other mesoblast, the permanent limbs are finally differentiated. It is probable, therefore, that the lateral limb-folds of this primitive type may be regarded as typifying almost completely the ideal form from which all of the various types of paired limbs have been evolved, as seen in the various groups. That such a generalized (not archetypal) ancestral form may be assumed to be represented by the most generalized Elasmobranchs, (Rays and Torpedos) will, I believe, be fully justified by the evidence, which remains to be offered in what is to follow.

While the method by which limbs are developed in Sharks and True Fishes, must be admitted by anatomists to be primitive, it must not be forgotten that long limbs of functional value, such as are possessed by Land Mammals, Birds and Reptiles, would be next to useless and an actual impediment in the struggle for existence, if appended to a fish. That this is true, is proved by the fin or paddle-like limbs of Plesiosaurs, Ichthyosaurs, Cetacea, Sirenia and Pinnipeds, in all of which there has occurred a gradual abbreviation, modification and even change of the position of the limbs, in order to economize the exertion of effort in a dense medium—water—in which short, fin-like limbs only would be preserved by *mechanical selection*. That is, the limb which presented the greatest mechanical advantages would be the one preserved, while its adaptation—modi-

fication in a determinate direction (not hap-hazard, through fortuitous variation,) would be conditioned by definite retroactions between the organism and its environment, and thus gradually stamp it with peculiar and mechanically advantageous features. This view should not be lost sight of; and, while it has been demonstrated to the satisfaction of all anatomists, (except P. Albrecht, whose views as to the primitive nature of the Cetacea are not borne out upon either morphological or palæontological grounds,) that, the aberrant forms alluded to above, are in all probability descendants of land and semi-amphibious types, we are forcibly reminded by these examples, of how the evolution of strongly marked types is directly conditioned by the peculiar nature of their specialized environment.

This brings us to the question of distribution in time, or the sequence of forms. Here, palæontology comes to the aid of the morphologist and affords the final proof that the Fishes are veritably the oldest of the limb-bearing vertebrates. The evidence derived from ontogeny, comparative morphology, taxonomy and palæontology is, therefore, in accord and quite conclusive as to the main fact of the primitiveness of the fish-like type, which is, therefore, the only one which can be regarded as affording the direct ancestral means through which the structural condition of the limbs of higher forms may be reached.

The mediate or indirect ancestry of the higher vertebrate types, was undoubtedly, one in which there obtained a condition even more primitive than in the most generalized of the limb-bearing fishes. Such a type was one which probably differed from the most generalized fish, in having the metameric elements of the paired limbs distinct for each segment; and not coalesced or fused into a more or less closely connected longitudinal series, covered by a simple, common fold of integument as in the latter. The only types which approach such a condition, are the existing Errant Annelids or Worms. These, or some peculiar generalized forms of Worms were therefore, the probable prototypes of the vertebrates as maintained by Dohrn and Semper, and, thanks to the brilliant researches of Bateson upon *Balanoglossus*, such a view has more in its favor now than ever before. Yet, here again the unwary must be cautioned, since *Balanoglossus*, living as it does buried in the sand, has probably undergone some retrogressive metamorphosis, so that it has been itself modified and diverted out of the path leading in the direction of the descent of the true vertebrate forms.

The presence of two lateral rows of vestigiary structures, in the position of parapodia, on either side of the tail of embryos of certain *Elasmobranchs*, and on either side of the dorsal median line, opposite the interval where the vertical dorsal fins are wanting, as first described by P. Mayer, led that investigator to regard such vestiges as *parapodoid* in character.

The existence of vestigiary structures of this kind, as well as their segmented or metameric relations, which are essentially the same in their general features, as those of the metameric elements of the limbs themselves, lends additional probability to the doctrine, that the vertebrates are the off-shoots of a worm-like ancestral form.

The suppression of the caudal parapodia or radial elements of the fins in the ancestral types, which led to the differentiation of the paired fins, may be ascribed to a number of other influences besides those referred to by Dohrn, of which the following may be mentioned,

1. If the ancestral type has been one which was at one time tubicolous in habit, the abortion of the caudal parapodia would be accounted for. Though, it must be admitted that this view is in the highest degree improbable, but not impossible.

2. The late outgrowth of the tail in annelids as well as in vertebrates, presupposes a belating of the functional activity of the caudal parapodia, through which their importance and development may have been hindered.

3. The slight use made of the parapodia of the tail as locomotive organs, after the tail became laterally flattened or compressed, since it is well known that the principal power of propulsion exerted by fishes, is by means of the alternate flexures of the tail; the fins aiding only in a moderate degree, their principal office being to balance or hold the body and keep it in the normal position. The exceptions to this rule are very few; the most important being that of *Mola* in which the dorsal and anal fins are the sole organs of locomotion, as shown by the writer elsewhere.

The abortion of the caudal part of the intestine, now represented by the post-anal gut, as it is termed by embryologists, may have had something to do with the development of paired limbs over the sides of what remained of the body cavity, as urged by Dohrn, but there must have been forces at work which led to this abortive process, by which the primitive gut was shortened. And, while it is undoubtedly a fact that such a shortening of the alimentary tract

has occurred, giving rise to the gutless and acelomatous tail of a number of classes, the shortening has been compensated for by the development of intestinal coils, diverticula, pouches, rugae, folds, follicles, crypts, glands, valves, etc., thus increasing the efficiency of the anterior portion of the alimentary canal as a digestive apparatus, so that the hinder part became useless, thus leading to its suppression. This seems to have been the cause antecedent to the one invoked by Dohrn.

Accepting the morphological part of the theory of Dohrn, as to the phylogeny and ontogeny of the paired and unpaired limbs, a difficulty has arisen as to how the parapodia became mainly dorsal and ventral, if, as is supposed, they are derived from an ancestry in which they were lateral. The view that the presence or absence of the alimentary canal was an efficient cause is beset with grave difficulties. A view which seems to me to be far more probable, rests upon the exaggerated development of a very different set of paired structures in the lower vertebrates, namely, the myotomes. The homologous tract in the Annelids is almost equally developed around almost the entire circumference of the somites, whereas in the vertebrates their development is almost wholly lateral, especially during the early stages. The bilaterality of the muscular system thus finding expression in the much thickened or laterally hypertrophied somatopleure of the primitive vertebrates, would inevitably crowd the notopodia and neuropodia of the ancestral Annelid, toward the ventral and dorsal edges of the body; the infolding of the medullary groove would divide the somatopleure in the middle line, and the growth forward of the stout notochord would tend greatly to aid from beneath, in breaking the continuity of the somatopleural layer across the median line. The suppression of the dorsal moieties of the body cavities in the myotomes would also aid in effecting the needed change.

With the advent of a laterally hypertrophied somatopleure, flexures of the body in the ventral or dorsal, as well as lateral direction would no longer be so well marked, and the habitual flexures of the body now established, would be alternating ones from right to left; thus, the habitual mode of flexure of the body of fishes would be attained. The mode in which muscular contractions resulting in the manifestation of movements would thus become more specialized than in the annelids and be brought to the stage observed in the lower vertebrata.

The less marked development or thickening of the somatopleure over the lateral and ventral parietes of the body-cavity, in the primitive vertebrates, would doubtless tend to affect the position of the notopodia, from which the paired limbs are supposed to be derived, causing them to retain their primitive place.

Thus far, only the ontogenetic theory of the limbs has been discussed, in order to prepare the reader for the evidence which is now to be presented; many of the data are from personal studies, and such old data as I have found available, I trust, will be brought into such contrast with the others, as a whole, as to bring out their morphological significance.

II. The proof of the inexact homology of the limbs of different types.

The inexact homology or equivalency of the limbs of different types of vertebrates has been suspected by authors, but no observations or systematic comparisons have been put upon record to show that there were good morphological grounds for such a conception of the nature of limbs. The exact morphological equivalency of the pairs of limbs of different types, would require that they arise from the sides of the same segments or somites behind the skull, for each pair, in all species of vertebrates. If, for example, the limb-bud of the pectoral or fore-limb arose from the fifth to the eighth post-occipital somites in all vertebrates, there could be no question that the fore-limb in one was the exact homologue of the fore-limb in every other form. Unfortunately, the facts of development and comparative morphology unequivocally compel us to admit that such is not the case.

1. Embryological evidence, considering especially the points of origin of paired limbs.

The positions in which the limb buds of the same pair arise in different types varies between wide limits, and, while there are causes which in part explain these variations, there are some complications involved which refuse any other explanation except that which supposes, that such variation in point of origin is an indication of inexact homology,

It may be stated as a general truth that, the paired nerves which go to a given limb have arisen from the somites, which were opposite or beneath the limb bud or fold, from which that limb developed. This may be shown to be true in the lower forms nearest the primitive type, from which all others may be supposed to have arisen. For example, the pelvic pair of limbs of physoclistous Fishes at first

grow out close behind the pectoral limbs, with little or no intervening space between them, but notwithstanding this fact, and in spite of an extensive subsequent translocation of the pelvic limbs forward into a position in advance of the base of the pectorals, the paired nerves which go to the pelvic limbs retain their primary origin behind those which pass to the pectorals. In the adult physoclists, therefore, the nerves going to the pelvic limbs, cross below those going to the pectorals, on their way to the pelvic limbs. This retention of the original nerve origins is in itself the best proof that we can depend upon to give us a clew to the groups of somites from which a given limb has arisen.

In many cases the origins of the paired nerves passing from the cord are much further forward than the foramina or intervertebral intervals which give them exit. This difficulty is probably quite explained away by the manner in which the vertebral canal grows in length compared with the cord. It is found, in fact, that the vertebral canal grows in length much faster, in many forms, than the cord, after a certain period. This causes the origins of the spinal nerves from the cord to appear as if they had been drawn forward some distance in advance of their points of exit from the sides of the vertebral canal. That this is a true explanation is proved by the fact that Kölliker has found the cord extending the entire length of the vertebral canal in the human embryo of three months, while the writer has found the same condition in the embryos of Cetaceans, two inches in length. It is, therefore, obvious that the cauda equina in these cases is developed at a later period, and as a result of the growth in length of the spinal or vertebral canal at a more rapid rate than that of the included cord itself. Similar phenomena occur in the cases of certain fishes (*Lophius*) and Goette has described the process in *Bombinator igneus*. In this last case, however, there is more or less positive atrophy of the posterior end of the cord in the course of development, so that only about 14 pairs of spinal nerves can be finally identified. In *Mola*, not only the cord, but the tail is also aborted to such an extent that only a very short, almost occipital, cord remains, the paired nerves passing directly to the lateral musculature of the vertical and paired fins, after forming a dorsal cauda equina. The cord in the long, flagelliform, reduced tail of the two *Lyomeri*, viz: *Gastrostomus* and *Ophiognathus*, shows unmistakable signs of atrophy or degeneration, in that the cord in the tail becomes so reduced to a mere flattened filament, that it is

with great difficulty that the white and gray matter can be distinguished in sections, or that any differentiation, except around the central canal, is visible.

In the singular and remarkable case of the Cetacea the embryological evidence, here offered, is entirely reconcilable with the views for the first time propounded by the writer upon morphological grounds, that the distal portions of the hind limbs are represented by the flukes. The latter being in reality the outward vestiges of hind limbs, so that the statement in recent text-books to the effect that, "the Cetacea are without hind limbs," must be qualified. The morphological evidence attainable proves beyond a reasonable doubt that the distal part of the hind limbs have been translocated backwards into their present position in Cetaceans, through the intermediation of a type approximating the existing pinnipeds, in which a similar process is now taking place.

In the Cetacea, the translocation of the hind limbs has been in a backward direction or just the reverse of what has occurred in the physoclistous Fishes. The Cetacean "lumbo-caudal plexus" which at least furnishes the sensory branches of nerves going to those organs, is therefore, either a backwardly translocated structure, similar in character to the forwardly translocated pairs of nerves going to the pelvic limbs of Physoclists, or it may be that they represent the modified posterior part of the system of spinal nerves, which supply the muscles of the powerful tail and have thus acquired secondarily a more intimate relation to the flukes. At any rate, the nerves, in this case, give us a far less potent argument in favor of translocation than do the skeleton and muscles, which are alone conclusive, when contrasts are made between their condition in the normal Mammalia, the pinnipeds and the Cetacea as the last extreme of modification.

But backward translocation of limbs is not confined to Cetacea. In all fishes so far observed by competent embryologists the pectorals grow out on either side of the anterior end of the trunk as a pair of folds just behind the last pair of branchial arches. In one group however, the embryology of which is not known, and which will in all probability remain inaccessible to us for the reason that, both *Gastrostomus* and *Ophiognathus*, the genera referred to, are abyssal forms, there is every reason to believe that the pectoral pair of fins has been translocated backwards. In the case of *Gastrostomus bairdii*, this translocation has pushed the pectoral fins

back out of their usual place, over about thirteen segments beyond the occiput, and the translocation of the pectoral of *Ophiognathus* is scarcely less. In both these cases the translocation is due to the extension backward of certain portions of the inferior arches of the skull, and of the mouth, as a result of which, the branchial apparatus and heart have also been displaced and lost their attachment or contiguity to the skull, while the carotid arteries have been lengthened to an extent which is altogether without a parallel amongst fishes.

Amongst median fins the anterior dorsal of *Lophius* is known to undergo considerable displacement forward, according to the published figures of A. Agassiz, showing the development of this form. Even in the history of the metamorphosis of the tail in heterocercal types, I have attempted to show (Origin of Heterocercy) that associated with the deflection upwards of the end of the caudal axis, due to a definite combination of mechanical conditions, there has also occurred a translocation forwards, crowding together of the inferior basal and hæmal supports of the caudal rays.

Turning again to the evidence, purely morphological and embryological, we find that the last pair of spinal nerves in *Phocæna* make their exit at the 45th vertebra, in Man at the 27th, in *Lepus* at the 29th, which facts when contrasted, sufficiently prove that there have been changes in the position of the source of the innervation of the limbs. The additional evidence which we possess showing that the hind limbs of the Cetacea and Sirenia have suffered displacement and may not be exactly homologous with the hind limbs of other vertebrates, consists in the fact that the hinder limb-buds (future flukes) grow out at the sides of the cylindrical tail and but slightly in advance of its termination, as low horizontal folds which have degenerated into the flukes, which now consist internally of the lowest grade of tissue, viz: fibrous connective, covered by the closely adherent integument.

In violent contrast to this we have the mode of development of the limbs of the *Physoclisti* at a parallel stage as buds or outgrowths immediately behind and with scarcely an interval between themselves and the rudiments of the pectorals immediately in advance of them. As a result of this, the paired spinal nerves which innervate the pectoral and pelvic limbs, form a continuous series with no interval whatever between them as shown by the accompanying table, while the greatest interval between the last brachial and first

lumbo-sacral nerve is found, as would be expected, in *Phocæna*, where it aggregates 16 pairs, according to the same table. We are accordingly forced to admit that the nerve supply going to a given limb is correlated with the position along the axis, at which it first grew out in the embryo.

If it is still insisted that these comparisons are unfair, I shall now propose some fresh difficulties to be disposed of by objectors to my thesis, that, pairs of limbs which are apparently exactly homologous upon superficial inspection are not necessarily the exact homologues of each other.

Take the cases of *Cottus* and *Esox*, if you please. We find here that in the first there is a continuous series of not more than seven pairs of nerves, reckoning from the occiput, which supply both the pectoral and pelvic fins. Turning now to *Esox*, we find five pairs of post-occipital nerves, which send a nerve supply to the pectoral, then follows an interval of twelve pairs of "intercostals," and it is only when we reach the 18th post-occipital pair, that we first find nerves which pass to the pelvic limb; eight pairs in all sending branches to that limb, so that, according to the old view, we have the preposterous conclusion that, the 25th pair of spinal nerves in *Esox* are the homologues of the 7th pair in *Cottus*!

We find in these two cases, moreover, that the rudiments of the pelvic limbs do not grow out at the same point, in respect to the median axis, but in the embryos of *Cottus* far in advance of the point of origin of the same fin in the embryo of *Esox*. And in proof of the fact that the pelvic fin of *Cottus* has not been derived by its migration forwards in the embryo, from a more posterior position similar to that in the embryo of *Esox*, we have the fact that we have no embryological evidence whatever, to show that such a translocation occurs. In fact, the rudiments of the pelvic fins grow out from the sides of the embryo in both genera in exactly the position required by the position of the nerve supply in the adults.

Further, is it to be supposed that in a Bird, where there are about ten post-occipital pairs of nerves which have nothing to do with innervating the wings, it would be fair to compare the first five of these which have no direct relation to the fore-limb, with the first five post-occipital pairs in *Esox*?

Here again, the embryological evidence is conclusive, since in Fishes generally, the pectoral fin-fold grows out immediately behind the last branchial arches and from what would be the cervical re-

gion in the bird, and *Esox* is no exception to this rule. In the Bird (Chick and Sparrow), I find, just as was to have been expected, that the pectoral limb-bud (wing) does not grow out from the sides of the cervical or anterior region of the trunk as in Fishes, but some distance behind it. In fact, a corresponding number of somites intervene between the hindermost limit of the cranium and the anterior margin of the fore-limb of the embryo bird. This gives to young embryos of birds their peculiar long necked appearance, because their necks are absolutely longer for morphological reasons than those of other warm-blooded vertebrates. We find indeed, that the fore limbs of birds are separated by a wider interval from the oral opening or the base of the skull, than those of Mammals. This fact will be palpably brought out, if two series of embryos of Birds and Mammals of approximately the same relative stages are laid side by side and compared. It will then be seen that the first traces of limb-buds in Birds arise farther back from the head than those of Mammals, thus clearly showing that the fore limbs, in the two cases, do not arise from serially equivalent somites,

The fore-limb of the Bird, therefore, grows out and develops at a point posterior to that at which the fore-limb of the Fish is developed; the segmental elements which enter into the formation of the fore-limb (pectoral) of the fish, are therefore not homonymous with those which enter into the formation of the fore-limb (wing) of the bird. Nor can less be said when we come to compare the early stages of the Bird and Mammal.

This failure of the limbs to arise from an exactly homonymous series of successive segments in different groups, shows in the clearest manner that such difference in origin unquestionably implies the existence of inexact homology, with all the morphological consequence which must follow.

We have also seen that sudden or rapid forward translocation of the hind limbs during their early stages, occurs only amongst Physoclists, where it has been repeatedly observed in different genera. In Cetacea, I have elsewhere sought to explain the peculiar method of their backward displacement in another manner, while the cases in which it is more than probable that the fore-limbs undergo rearward displacement include only one type of Fishes viz: the Lyomeri. In no others except Pinnipeds does there appear to be the slightest evidence of the occurrence of translocation. The defenders of the Archipterygium hypothesis are, therefore, so far as they would avail

themselves of the theory of the translocation of the limbs, left with nothing to rely upon. Even supposing that the phylogenetic history is inaccurately repeated in the ontogeny of the forms here used in illustration, how will we explain on such a supposition, the persistent posterior origin of the pelvic limbs in Physostomes from folds separated by an interval of as many as 20 somites from the pectorals, while in Physoclists there is either a very small interval or almost none; and why is it that the nerve supply for the limb should be derived so constantly from the pairs underlying the point of origin of the limb-fold? We saw, moreover, that when translocation did occur during ontogeny, that the distal portion of the nerve supply was carried along with the limb, while the point of the origin of the nerve supply remained unchanged. The other cases of translocation, which are well made out, the Cetacea and Lyomeri are not fairly to be contrasted with that of the Physoclisti, because, in the first instance the hind limbs have become totally incapable of free or independent movement, while in the case of the Lyomeri, the fore-limbs have become detached from the cranium, and limb and pectoral arch so undeveloped as to present a condition which is attained by many fresh-water forms before they leave the egg. The Cetacea, Lyomeri and Ichthyosauria, are the only vertebrates in which the pelvic or pectoral girdle has suffered displacement, detachment or reduction, except the Physoclisti, and, while it must be admitted that our information as to how this occurred, is for the most part only inferential and based upon comparative studies of the morphology of allied forms, as far as regards the first three, the actual observation of how such a process *has* occurred in the last named group should make us all the more ready to expect equally remarkable revelations regarding the others. And of fossil groups besides the Ichthyosauria, it is not impossible or improbable that such as the Enaliosauria and others, might afford profitable and suggestive contrasts. These, however, we can have little hope of studying from the stand-point of the embryologist, owing to the paucity of material.

The embryological evidence has now been stated, together with such a discussion of the extent to which translocation of the limbs, during their early stages, has had any bearing upon the questions at issue, so that we may at once turn to the consideration of the morphology of adult forms in this connection.

2. *Anatomical evidence, considering especially the relations of the spinal nerves to the limbs.*

In order to make comparison easy between the various adult types, I have tabulated the pairs of nerves which enter into the composition of the brachial and lumbo-sacral plexuses, or, as we may name them for brevity's sake—*proplexus* and *postplexus*, in such a way as to show their inexact homology and homonymy at a glance. The pairs of nerves belonging to the *proplexus* are indicated by the sign x , while those belonging to the series of the *postplexus* are indicated by the sign o ; these signs are also placed in the successive columns from left to right in such an order as to indicate at once the serial number of the nerves they stand for, as reckoned from the occipital foramen towards the end of the tail.

The relations of the *proplexus* and *postplexus* may be graphically represented by such a table and it is evident from a simple inspection and comparison of the limb-innervating series of spinal nerves indicated by the arbitrary signs, that there is clearly a lack of homonymy of the paired limbs, if the determination of such homonymy depends upon the origin of the paired limbs from somites, which are distant the same number of segments from the occiput or posterior extremity of the head.

The thirty-two pairs belonging to the *proplexus* of *Raia eglanteria* cannot by any possible supposition be made equivalent to the third and fourth nerves entering into the *proplexus* of *Rana*; nor can it be shown that the *proplexus* of *Raia* is exactly homologous with that of *Esox* or *Cottus*. Even supposing that every two or three pairs of *Raia* represent morphologically, but a single pair in *Rana* and *Esox*, the difficulty is not disposed of, because, while it is possible to suppose that one-half of a given number of somites in a Selachian, represent a morphologically equivalent number in Teleosts or Amphibia, there is no valid ground anywhere discoverable in morphology, for supposing that the ratio of the morphological equivalency, when the values of the somites of the two types are contrasted, is greater than this. This contrast, however, does not avail, for even upon such a supposition, one-half of the number of nerve pairs in the *proplexus* of *Raia* is sixteen, or eleven more than in *Esox*.

The utter absurdity of this last way of bringing the *proplexuses* of *Raia* and *Esox* into homonymical agreement is brought out, if we make another contrast. In fact, it is possible to show that, if we push the theory of multiples too far that we cannot account for the relations of the *postplexuses* of a Physostome and a Physoclist. For, suppose the thirty-two pairs of the *proplexus* of *Raia eglanteria*

fused by fours into eight, this brings the first pair of the post-plexus into the position of the ninth, but in the Physostomous *Esox*, the first pair of the post-plexus is the 18th, while in some Physoclists, the first pair of the post-plexus is the fourth or fifth, a result which makes the absurdity of such a method of reasoning still more preposterous. The climax is reached when the theory of multiple equivalency is resorted to in comparing the post-plexus of *Raia* and *Esox*. The thirty-third to the forty-sixth pair in *Raia*, fourteen in all, would be equal to about three, or a little more, pairs in the post-plexus of *Esox*, on the basis of the doctrine of multiples. This is four less than the required number in *Esox*, besides which, the first pair would be brought into the position of the ninth instead of the eighteenth, its required place. Or if we took two pairs of spinal nerves of *Raia* to equal one of *Esox*, we should only have seven for the post-plexus of the latter or one less than the required number, while the first would be brought into the position of the seventeenth instead of the eighteenth, its required position.

The table also shows that the proplexus of *Raia batis*, according to Swan, is nearly equal to the pro-and post-plexuses of *Raia eglanteria* taken together. It is also shown that the proplexus of *Mustelus canis* is made up of not quite half as many nerve pairs as that of *Raia eglanteria*, and it therefore has just a third as many as *R. batis*. In that it is now known that each anterior somite gives off just twice as many muscular buds as there are somites, the buds corresponding to as many rays, it is clear that the anterior fins of these three Elasmobranchs are not the exact homologues of each other, that is, the pectoral of *Raia* is derived from more somites than that of *Mustelus* and they can therefore not be equivalent in an exactly homological sense.

A still further inspection of the table will enable the reader to make many other comparisons which will be equally striking. Amongst the others, that of *Phocæna* is one of the most interesting. It will be seen that the post-plexus is pushed backward. But this may be partially accounted for, as only the first five pairs can be fairly compared with those of other Mammals, this plexus in *Phocæna* as a whole, having undergone reduction, the thirty-first to the forty-fifth pairs forming what ought, perhaps, to be considered a caudal plexus.

Throughout, it will be seen that from the Amphibia onward, the number of nerve pairs entering into the formation of the plexuses, have undergone as marked and abrupt a reduction in number, as the

radii or digits, in the transition from the many-rayed fishes. This is a very significant fact and is of striking importance, as indicating that there is a certain general correspondence between the number of nerve pairs and the number of digits in the heptadactyle, (=what was formerly considered the pentadactyle) limb of higher vertebrates, since the identification of extra, but vestigiary radial, ulnar, tibial and fibular digits by Bardeleben. The seven digits of the manus never much exceed the usual five, to six pairs of the proplexus, while the seven digits of the pes do not much exceed or fall below the six to nine nerve pairs of the most usual type of postplexus. We saw too, that in those cases where an excessive number of digits were developed in the fore-limb, as in the case of *Raia*, there was an exact correspondence in the number of nerve pairs of the proplexus. The exactitude of this correspondence is in fact, apparently, in proportion to the degree to which the digital elements—radii (of the pro- meso- and metapterygium) have retained their archaic composition, relation, want of torsion, etc., in either limb,

3. *Fusion of radii to form the pro- meso- and metapterygium and their inexact homology.*

On the basis of the doctrines established by Dohrn, through ontogenetic research, it is quite safe to assume with him, that the three basal elements of the limb in Elasmobranchs have been derived from the primitively separate cartilaginous radii, developed in the mesoblastic tissue between the muscular limb-buds thrown off by the somites. The different genera of Selachians, however, show that the pro- meso- and metapterygium, as suspected by Wiedersheim, are probably not exactly homologous, because the mesopterygium is not always present, and when present, upon comparing any pair of genera, it will be found that in no two do the number of radii present in the pro- meso- and metapterygium correspond. This difference is apparently due to the fact that the number of radii in the whole limb, in different genera, is not constant, as already pointed out. Furthermore, it is evident that the pro- meso- and metapterygium respectively, cannot be of the same morphological value in different genera, if the same number of somites do not take a share in the formation of each of these three parts in different genera. It follows from this that neither the uniserial nor biserial archipterygium of Gegenbaur and Huxley can be made to yield such a fixed hypothetical type as will lead up to the various modifications of the paired

limbs, because it can be shown that what is metapterygium in one case is not such in another; besides, there are embryological difficulties in the way which are insuperable. The exact homological equivalency of pro-meso- and metapterygium, has in fact, been abandoned by some of the ablest contemporary anatomists.

4. *Formation of plexuses and their inexact homology.*

There is no more reason to suppose that the nerve plexuses of vertebrates are exactly homologous, than there is for the supposition that the muscles are exactly homologous. The trapezius and latissimus dorsi for example, cannot be regarded as having exactly the same morphological value in Man, Selachians and Amphibians, because in these three cases they are not derived from the same number of somites; they are only physiologically homologous.

The arguments of Gegenbaur, Fürbringer and Davidoff that the limbs have migrated backwards or forwards, as indicated by the existence of the collector nerves formed by the ansæ and commissures between successive pairs, anterior and posterior to those pairs which form the functional plexus of the limb, are not sustained by embryological evidence, and the existence of the *nervus collector* is rather to be taken as evidence that the radii belonging to the pairs entering into the anterior and posterior portion of the *n. collector* have been suppressed or fused with the radii forming the peduncle of the limb. My reason for holding this opinion is, that the only case in which the effect of translocation of a limb on the peripheral ends of the nerve pairs passing to that limb, has been traced embryologically, shows that their peripheral ends travel with the displaced limb, at the same time retaining their origins, and do not run parallel for a long distance with the functional pairs, as is shown by Davidoff's own figures of the nerve plexus of *Acanthias*.

Whatever fibres of the collector nerve enter into the plexus of the functional limb, have been incorporated in virtue of the constriction of the limb fold posteriorly and anteriorly, as a result of which many radii which were originally attached to the sides of the body, have acquired a secondary attachment to the proximal ends of the blended radii, from which the so-called pro-meso- and metapterygium have been evolved. There can be no doubt of the fact, that in this way the limbs of primitive vertebrates first became pedunculate. It can thus be shown that the radii which are detached from the body, are not lost but simply carried farther out by the accelerated growth of the radii forming the skeleton of the peduncle of the limb. This

type of displacement of positions of a limb, cannot fairly be compared with the case of the Physoclists, in which the peduncle of the limb also shifts its position in reference to the origin of its nerve supply. The foregoing view as to the origin of the *n. collector*, has, I would state here, been arrived at independently by Wiedersheim in the second edition of his *Lehrbuch*, (p. 323).

It might also be added that, wherever the proplexus and postplexus are parts of a continuous series of pairs as in *Raia*, the fin-folds of both pairs of limbs are also continuous at the time they first grow out, whereas, when they are not continuous, and when the anterior and posterior limbs grow out as more or less widely separated folds, but with abortive limb-buds intervening, which never form a part of the permanent limb, as may be observed in the embryos of *Mustelus*, the two plexuses are separated by an interval.

Such forms as *Raia*, also exhibit extensive fusion of the proximal ends of the separate radii, leading to the formation of the longest possible type of pro- and metapterygium, whereas in the types like *Mustelus*, the propterygium and metapterygium are composed of fewer radii. They cannot, therefore, be homologous and we cannot on that account take any metapterygium or propterygium or whole fin of any particular type, as the ground form from which an ideal archipterygium or cheiropterygium may be supposed to have arisen. It is probably better for the present to assume, for the reason that an inexact homology exists when the limbs of different vertebrates are critically compared, that the different types of limbs, as we now see them in the higher groups, have arisen independently and differently in the different phyla. That the manus and pes, as seen in the various vertebrates, from Amphibians upward, show a common plan there is no doubt, but of the fact that similar structures may originate independently of each other, we have numerous instances in the animal kingdom.

It is not even certain that there may not be more than two pairs of limbs developed in certain Fishes. In the cephalic fins of *Torpedo* and *Narcine*, the radii rest upon the rostral cartilage of the cranium, thus separating them from the shoulder girdle. This attachment is supposed by Gegenbaur to be a secondary one, the radii of the cephalic fins being part of the radii of the propterygium, secondarily detached from the anterior portion of the pectoral. But for this opinion there do not seem to be more valid grounds, than for the supposition that the cephalic fins are outgrowths of the head, since

it is known that in some *Dipnői*, the pectoral limb is innervated partly by branches from the hypoglossus and vagus, (*Protopterus*).

In the domesticated races of the Japanese Gold-fishes, popularly known as "Fan-tails," in which both the anal fin and the ventral lobe of the caudal fin are frequently double, it has been shown by Mr. S. Watase that they arise from a pair of parallel ventral fin-folds extending from the hinder part of the yolk sack to the end of the notochord. He has further shown in the same memoir* that the double, ventral series of interhæmals of the anal and caudal of these fishes are the supports of the radii derived from actinotrichia and the cartilaginous nodules at their bases, thus bringing these fins into complete morphological harmony with the ventrals, in which the pelvic girdle is probably to be considered as representing modified interhæmals. It indubitably follows from this, that the double or paired anal and the double inferior lobe of the caudal, are to be considered as paired fins or limbs serially homologous with the pectoral and pelvic pairs. While this embryological and morphological evidence most admirably confirms the views of Dohrn as to the nature of the paired limbs, there can be little doubt that, the double anal and caudal have a just claim to be regarded as additional pairs of limbs, making four pairs in all. Their development is further to be regarded as due to reversion induced by a process of degeneration, which has affected the whole urosome or tail of these fishes from the vent backwards. This degeneration seems to be due to domestication, since it is now admitted by an expert American breeder of these varieties of gold-fishes, Mr. W. P. Seal, that the forms most modified and prized by fanciers can only be reared in restricted quarters or in aquaria or protected pools of moderate dimensions. The extreme shortening and modification of the muscular and axial parts of the tail, has been produced in the course of a prolonged process of selective breeding, their singular changes of form being probably due to disuse. The most modified forms which the writer has seen alive, were slow and sluggish in their movements, their enormously lengthened caudal, pectoral and ventral rays and membranes seeming to interfere with any rapid motions. The shortening of the muscular portion of the tail would also aid to produce such a result, as is known from Strasser's experimental researches on the function of the tail in fishes.

*On the caudal and anal fins of Gold-fishes. Journ. Science College, Imperial University, Japan. Vol. I.

The degenerative processes made manifest in ontogeny, often undo the synthetic or constructive morphological work, which has been accomplished during phylogeny. This seems to be the case in these extremely modified forms of Gold-fishes, in which, indeed, there is palpable evidence of great cranial modification, similar to that seen in domesticated races of Pigs and in the Japanese Lap-Dogs (*Dysodus*, Cope), in all of which, as in these fishes, the anterior cranial and facial bones have been greatly modified.

The preceding explanation seemed necessary in order to emphasize the doctrine that paired fins might be evolved from the sides of the tail as supposed by Dohrn and Mayer, by the median fusion of the ventral fin-folds, which, according to their views, were primordially double and lateral. It follows from this doctrine, that the nerves passing to the musculature of the anal and caudal pairs of fins, must be considered as forming two additional plexuses, neither of which can by any mode of torturing the facts, be rendered homologous with those which supply the pectoral or ventral pairs.

III. Consequences of the preceding data.

The facts presented above seem to me to lead to the conclusion that the ichthyopterygium in Fishes is very far from representing the same or homologous structure; a view which the ontogeny of the higher vertebrates fully confirms. While the first point has been admitted by Mivart, Huxley and others, the second has not received the attention which its importance demands. The fact that the rudiments of the paired limbs do not normally arise in a homonymous position or at the same points along the axis in Mammals, Birds, Reptiles, Amphibia, etc., and without any manifest action of translocation during development, seems to the writer to preclude the possibility of our assuming that there has existed a common and exactly homologous, ancestral chiropterygium, from which the limbs of vertebrates, from Amphibians upward, have been evolved. There are many difficulties in the way of an answer to this question. First of all, the universally admitted fact that similar structures may be developed under similar conditions in widely dissimilar types. Secondly, the utter want of exact homology when the pro-meso- and metapterygium are compared. Thirdly, the few unassailable facts which we possess in regard to undoubted instances of the translocation of limb rudiments. Fourthly, the origin, by coalescence, of an indefinite number of radii to form the pro-meso- and metapterygium. Fifthly, the variations to which this coalescence is subject; that is,

posterior radii may be swept forward proximally or anterior ones may be swept backward proximally; or both processes may occur simultaneously; or certain radii may be so accelerated in their growth and others so retarded as to give rise to a uniserial or biserial pedunculate limb. Sixthly, the evidence as to occurrence of the abortion and extensive loss of radii in any part of the ichthyopterygium is clear, as well as the frequent dichotomous subdivision of the distal ends of single radii* as in the pectorals of *Raia*, and cephalic fins of *Torpedo*. Such secondary or divided radii may indeed be homologous with the digits of higher forms, as it seems might be countenanced by the fact that the limbs of some Amphibia have but two digits at first, and that the others afterwards bud out at one side or edge as was first noted by Prof. Baird, and subsequently confirmed by Cope and Baur. Such a view is also to some degree countenanced by the manner in which supernumerary digits develop in Amphibia and by the simple structure and variability of the manus and pes of *Amphiuma* or *Muraenopsis*. Seventhly, the obviously compound nature of the mesopterygium of *Polypterus* as is proved by the presence of serially or segmentally arranged foramina, perforating it for the passage of nerves, and which has been supposed to be shoved outward to give rise to the intermedium, which in the chiropterygium, must accordingly represent twelve fused radii, whereas, it ought not at most, represent more than three or four. Eighthly, the lack of correspondence or agreement in the structure of the tarsi and carpi of higher forms, some of which are believed to present traces of not less than six digits; and in others as many as seven, and the impossibility of determining with absolute certainty, the homologues of the tarsal and carpal bones, as the *centrale* is sometimes represented by two elements or is so obscured as to be too indistinct to be clearly made out; the same may be said of the *intermedium*. Ninthly, the impossibility of determining from which border of the primitive fold the elision or abortion of radii first began, owing to the fact that the torsion of the fold on its own base, does not always appear to occur or at least is not recapitulated, this torsion varies from 90° to nothing at all. Whether the suppression of radii was metapterygial or propterygial at first, we cannot now determine with certainty, and all that we can justly say is, that it has probably occurred on both borders in various types, and to the extent of a

*The radii of Elasmobranchs as here understood are in no sense the homologues of the rays of Teleosts, which are mainly derived from actinotrichia.

variable number of radii in different cases. Tenthly, if the digits of higher forms represent the distal extremities of one or two dichotomously divided single rays, each derived from a single somite, it is not possible to state with certainty to which order of secondary branches they belong, because the epiphyses and diaphyses of the proximal long bones may represent elements which should be taken into account. The digits would probably represent the second subdivision, if the epiphyses of the long bones were thrown out of the reckoning.

The following suggestion seems very important. The manifest impossibility of deriving a chiropterygium from a given or known uniserial or biserial ichthyopterygium, which will serve as a starting point for the limbs of all known higher vertebrates, forcibly impresses the conclusion that, firstly, the limbs of all vertebrates are not necessarily exactly homologous and that, secondly, the chiropterygium has in all probability been independently developed several times and indirectly from different segments along the sides of the primitive vertebrate body.

The importance of this conclusion, as qualifying the prevalent doctrines regarding the homologies of the limbs of vertebrates, may be inferred since it has been found by Albertina Carlson (Kongl. Svensk. Vet. Akad. Handl. xi, 1887,) that in the Ophidia the postplexus may be developed opposite the intervals between the 275th, to the 278th, vertebræ. Besides this, Miss Carlson has shown that there is great variation in the position of the postplexus in different genera of Ophidians.

It seems almost unnecessary to note here, that the modifications of the position of the limb in reference to the same segments along the body, also implicates the homologies of the muscles and blood vascular supply.

The view which has been suggested above as to the origin of the limbs of the higher vertebrates, implies that the distinction between the uniserial and biserial archipterygium is simply formal; that whether a fin shall become provided with series of radii on one or both sides depends on the manner in which coalescence of the primary radii took place; whether, in fact, from one or both borders. The usual type in Elasmobranchs occurred by coalescence from behind. In *Raia* coalescence occurred from both the anterior and posterior borders of the pectoral as shown by its ontogeny, giving rise

to a uniserial (anterior) propterygium, and a similar (posterior) metapterygium.

The cause of such coalescence has been in part, that other adjacent functionally active parts pressed upon the radii which were growing at an accelerated rate. The mode in which the radii composing the fins were functional was also active in promoting coalescence, in fact, there is no reason to doubt that almost exactly the same arrangement of forces was potent in inducing the displacement forward of the proximal ends of the posterior radii of the pectoral and pelvic fins, as in the case of the caudal, as the writer has attempted to show in his essay on the origin of heterocercy. This is also strikingly shown in the dorsal and anal fins of some species. The increased pressure or resistance exerted by the surrounding water on the hinder lower quarter of the vertical or lateral fins while in action would constantly tend, owing to the peculiar flexures assumed by the surfaces of the fins while in motion, to shove the hinder border forwards and carry the basal ends of the hinder radii forwards. The method of this might be shown by means of a diagram, in which the force exerted by the fin was one side and the resistance of the water the other side of a parallelogram of forces, while the direction in which the base of the fin was constantly tending to be displaced, would be determined by the resultant acting against the hinder lower margin of the fin. The alternating direction of the stroke of the fin does not impair the efficiency of this set of active forces, but makes them more efficient, since, though the action of the forces is alternately reversed as respects the directions in which they act, the effect is the same.

This hypothesis of the origin of the uniserial fin applies to all its types, whether encountered in the dorsal finlets of *Polypterus* or in the paired fins of Elasmobranchs, Chondrosteans and Chimæroids. It also leads up to a more comprehensive theory of the origin of all the modifications of the fins, as seen in the diverse types of fishes.

As to the chiropterygium, we are warranted in the affirmation that, whether it has arisen from the dichotomous division of the distal portion of a separate and single ray, or of two rays, or by the modification of the distal radii of a uniserial metapterygium, or of the distal end of a biserial metapterygium, our difficulties are pretty much the same. And, while the view that those limbs which seem to show traces of the plan of the chiropterygium, have probably arisen from some type approximating the metapterygium of some Elasmobranchs, we must admit that we cannot, for lack of evidence,

specify the particular type of metapterygium and over what particular somites it was primarily attached, nor even, indeed, that particular radii, with terminal dichotomous divisions, may not have been equally well adapted to furnish the morphological foundation of the chiropterygium and the endless variety of terminal modifications of the fore-and-hind-limbs of the higher vertebrates.